Paleobiology, 34(1), 2008, pp. 104–116

A sampling-adjusted macroevolutionary history for Ordovician–Early Silurian crinoids

Shanan E. Peters and William I. Ausich

Abstract.—Temporal variation in sampling intensity and geologically controlled rates of fossil preservation distort macroevolutionary patterns in the fossil record. Here, we use a comprehensive, list-based compilation of taxonomically and stratigraphically vetted global crinoid genus occurrences to evaluate and correct for the effects of variable and incomplete sampling from the Ordovician through Early Silurian. After standardizing the number of occurrences or the number of biofacies used to estimate the stratigraphic ranges of genera and after adjusting rates of turnover to account for the incomplete preservation of true extinction and origination pulses, we find support for several important revisions to the macroevolutionary history of crinoids. First, in contrast to the uncorrected data, sample-standardized genus richness does not appear to increase by more than 20% after an abrupt Middle Ordovician (Harnagian) diversification. Second, the only significant short-term change in genus richness following the Harnagian increase is a ≥24% decline from the Rawtheyan to the Hirnantian. Third, volatility in rates of genus extinction is increased after adjusting for preservation and there remain significant peaks of extinction in the Rawtheyan, which marks the end-Ordovician extinction, and in the middle of the Early Silurian. Finally, significant increases in origination rates occur in the Early Silurian. These results reaffirm the importance of the end-Ordovician extinction for crinoids, but they also highlight the comparatively poorly sampled Early Silurian as a time of turnover among crinoids.

Crinoid genus extinction rates are positively correlated with area-weighted rates of sedimentary package truncation, suggesting that extinction may have been controlled by physical environmental changes, such as the contraction of unique epicontinental sea habitats. The lack of a correlation between genus origination and sedimentary package initiation reinforces this hypothesis and suggests that other factors, such as evolutionary innovations and biotic interactions during the Ordovician radiation, may have been more important in controlling the diversification of crinoids.

Shanan E. Peters. Department of Geology and Geophysics, University of Wisconsin–Madison, Madison, Wisconsin 53706. E-mail: peters@geology.wisc.edu
William I. Ausich. Department of Geological Sciences, 125 South Oval, Ohio State University, Columbus, Ohio 43210. E-mail: ausich.1@osu.edu

Accepted: 11 October 2007

Introduction

Two major types of bias distort macroevolutionary patterns in the fossil record: those that are intrinsic to the scientific process of accumulating knowledge, including socioeconomically induced discrepancies in geographic sampling (Sheehan 1977; Kiessling 2005), incomplete sampling (Signor and Lipps 1982; Foote 2000), and taxonomic and stratigraphic errors and inconsistencies (Smith and Jeffery 1998; Adrain and Westrop 2000; Ausich and Peters 2005), and those that are extrinsic to the scientific process and inherent in the geological record itself, such as rock quantity and availability (Raup 1976; Smith 2001; Peters and Foote 2001; Crampton et al. 2003; Peters 2005), sequence architecture (Holland 1995, 2000; Smith et al. 2001), geographic distribution of rock (Allison and Briggs 1993), and taphonomic and diagenetic factors (e.g., Kidwell and Holland 2002; Cherns and Wright 2000; Wright et al. 2003). If all of these biases were uncorrelated, of comparable magnitude, and randomly distributed in time and among taxa, then macroevolutionary patterns derived from the fossil record would be noisy and diffused by incomplete sampling (Signor and Lipps 1982; Foote 2000), but they would not be fundamentally distorted. However, both intrinsic and extrinsic biases are known to change over time, and many biases are likely to be correlated, a situation that could render many face-value macroevolutionary patterns little more than complicated artifacts.

Although no study has yet addressed simultaneously every conceivable source of bias, there have been numerous efforts to quantitatively test or correct the effects of

0094-8373/08/3401-0007/$1.00

some intrinsic biases (e.g., Adrain and Westrop 2000; Jeffery 2001; Ausich and Peters 2005), some extrinsic biases (e.g., Holland 1996; Holland and Patzkowsky 2002; Peters and Foote 2002; Peters 2005, 2006a), or some combination of the two (e.g., Miller and Foote 1996; Alroy et al. 2001; Smith et al. 2001; Foote 2003, 2005; Crampton et al. 2006; Kiessling 2006). Here, we use a comprehensive, taxonomically and stratigraphically vetted global compilation of Ordovician-Early Silurian (O-ES) crinoid genus occurrences to estimate the magnitudes of intrinsic and extrinsic biases and to then remove those biases by standardizing sampling effort. We also estimate the probability of sampling a crinoid genus in each time interval and then use those probabilities to find the best-fit true extinction and origination histories using a survivorship-based rate optimization procedure (Foote 2003). Finally, we compare the macroevolutionary history of crinoids to quantitative measures of the rock record in order to evaluate extrinsic biases and to explore possible causal mechanisms for the newly documented evolutionary patterns.

Crinoids constitute one of the defining clades in Sepkoski's Paleozoic Evolutionary Fauna (Sepkoski 1981) and are important components of many post-Cambrian Paleozoic marine communities. Understanding the dynamics of crinoid macroevolution is therefore important both in its own right and because it is likely to be relevant to other Paleozoic epifaunal suspension feeders. We have chosen to focus on the O-ES interval because it includes the second most severe mass extinction in the face-value fossil record of marine animals (the end-Ordovician mass extinction; Sepkoski 1981; Raup and Sepkoski 1982) and because the O-ES is thought to be pivotal in the evolution of many marine organisms, including crinoids (e.g., Eckert 1988; Donovan 1988, 1989; Baumiller 1993; Ausich et al. 1994; Eckert and Brett 2001; Droser and Finnegan 2003). In addition to the mass extinction at the end of the Ordovician, the O-ES also marks the first major macroevolutionary turnover between crinoid evolutionary faunas (Baumiller 1993; Ausich et al. 1994).

Data and Methods

Data Compilation.—Crinoid occurrence data were gathered from the systematic literature, which is easily accessible using Webster (2003), the Paleobiology Database (http://paleodb.org), and first-hand experience of the authors. Crinoid species assemblages were compiled globally for the entire Ordovician and Llandovery. Data derive primarily from species that are recognized by calyx and arm morphology, but, in rare instances, genera identifiable on the basis of isolated columnals (e.g., the square columnals of *Xenocrinus*) were included.

Valid crinoid species occurrences were given updated genus assignments and then compiled into lists representing an assemblage of known fossils from a limited stratigraphic and geographic setting. For example, all crinoid species that have been described from the Lebanon Limestone (Guensburg 1984), which outcrops over a relatively limited area in the Nashville Dome (Holland and Patzkowsky 1998), were compiled into a single list of species occurrences. The age of each biofacies was then determined by using up-to-date correlation schemes, not ages reported in the original references, which can be incorrect (Ausich and Peters 2005).

The term ''biofacies'' is here used to describe the crinoid lists because they do not typically represent single field censuses. Instead they approximate the environmental and spatial scale of a biofacies and represent the cumulative efforts of one or more taxonomic specialists. In cases where a single biofacies spans two or more time intervals, separate biofacies were identified for each. This protocol is largely a methodological convenience, but we believe that subdividing biofacies that span more than one time interval accurately reflects the distribution of crinoid genus occurrences within each of the time intervals used here (see below).

Although taxa with multi-element skeletons are often assumed to have a poor fossil record in comparison to more robust taxa, such as brachiopods, the data used here allow several important biases to be circumvented, or at least standardized. For example, because cri-

TABLE 1. Time intervals used in this study.

Time interval	Abbreviation	Age of base	Duration (Myr)
Telychian	T	436.0	7.8
Aeronian	A	439.0	3.0
Rhuddanian	R	443.7	4.7
Hirnantian	H	445.6	1.9
Rawtheyan	R	447.4	1.8
Cautleyan	C	449.0	1.6
Pusgillian	P	451.0	2.0
Onnian–Actonian	O	453.6	2.6
Marshbrookian	M	455.8	2.2
Soudleyan	S	456.9	1.1
Harnagian-Costian	H	459.0	2.1
gracilis Zone	g	460.9	1.9
teretiusculus Zone	t	463.7	2.8
murchisoni Zone	M	464.8	1.1
bifidus Zone	b	466.2	1.4
hirudo Zone	h	470.8	4.6
extensus Zone	E	478.6	7.8
Late Tremadoc	Trem-u	485.5	6.9
Early Tremadoc	Trem-1	488.3	2.8

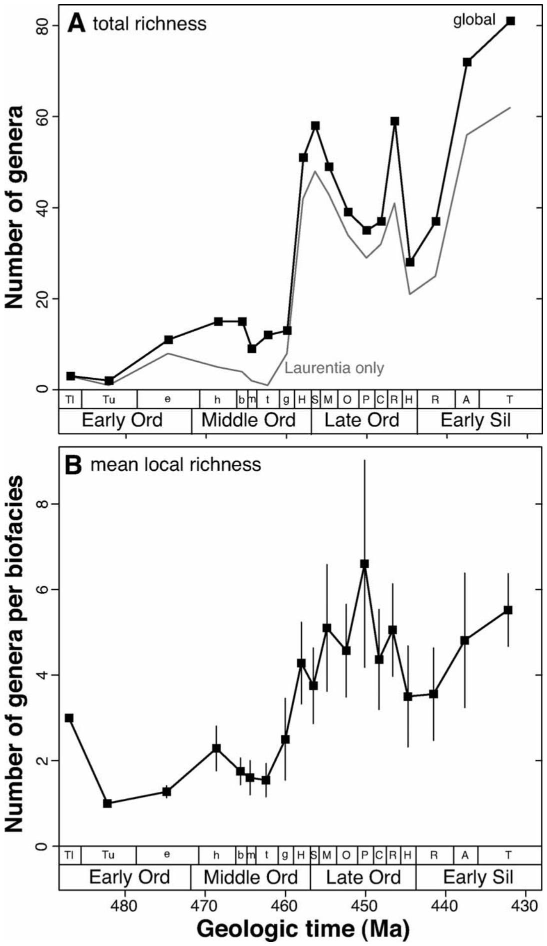

FIGURE 1. Uncorrected crinoid genus richness. A, Total global crinoid genus richness (range-through richness) for 19 Ordovician and Early Silurian time intervals (stages; see Table 1 for abbreviations). Gray line shows total richness for Laurentia only. B, Average genus richness in biofacies (i.e., list length). Error bars show ± one standard error of the mean. A total of 1057 global occurrences from 264 genera were used to generate the time series. Data plotted at age of interval midpoint.

noids and other echinoderms disarticulate soon after death (Blyth Cain 1968; Meyer 1971), taxonomically informative articulated echinoderm assemblages are commonly preserved only when storm-suspended sediment settles rapidly over large areas of seafloor (see Ausich 2001 and references therein). Thus, postmortem transport, current sorting, preferential destruction of fragile taxa, and other taphonomic biases that influence the composition of more time-averaged fossil assemblages are typically much less of a factor in crinoid assemblages containing fossils identifiable to the species or genus level, even if the formation of such assemblages occurs infrequently.

Each biofacies was assigned to one of the substages defined by Fortey et al. (2000) and summarized in Table 1. We chose these intervals because they can be readily correlated globally (S. Bergström personal communication 2007) and because they correspond to newly proposed Ordovician stages (Finney 2005; Bergström et al. 2006). Median interval duration is 2.2 Myr. To avoid accentuating edge effects, a place-holding time interval was also included for all of those crinoid genera that are known to survive past the Llandovery.

We must emphasize that although our crinoid database is as comprehensively global as the existing taxonomically informative literature permits, of 1057 total genus occurrences, 876 (83%) derive from Laurentia (gray line, Fig. 1A) and 120 (12%) derive from Avalonia, Baltica, and southwestern Europe. This geographic distribution is unlikely to reflect the true distribution of crinoids during the O-ES. Instead, the North American and European preponderance of data reflects a long-recognized socioeconomic bias in most of the easily accessible paleontological literature (e.g., Kiessling 2005). Ideally, geographic sampling inequality could be addressed by conducting separate analyses for each paleocontinent and by standardizing the spatial component of sampling intensity, but there are presently too few crinoid occurrences outside of North America and Europe for this to be feasible. Thus, the results presented here must be interpreted as applying primarily to North American and European crinoids.

Sampling Standardization.—Ideally, when trying to measure macroevolutionary patterns through time, an equal number of equally spaced fossil specimens would be collected in every time interval. Times of first and last appearance and occurrences between range endpoints would then be derived from the pooled and standardized data. Macroevolutionary parameters would then be estimated from the standardized samples and then adjusted for the forward and backward smearing of true origination and extinction pulses due to incomplete sampling (Foote 2000, 2003). Unfortunately, such a standardized approach is rarely feasible. Instead, macroevolutionary patterns are typically inferred on the basis of an unknown number of fossil specimens that are compiled into lists of taxa (occurrences) for a given location. The number of lists, the number of occurrences in those lists, and the underlying number of specimens used to construct the lists typically vary through time, thereby introducing sampling artifacts. Alroy (2000) provided a thorough treatment of the various analytical approaches to standardizing sampling for list-based occurrence data. Bush et al. (2004) returned to Alroy's (2000) work in order to reiterate his methodological innovations, revisit the underlying assumptions, and challenge the interpretations of Alroy et al. (2001) on the basis of the occurrence weighting scheme (see below).

Here, we attempt to remove the effects of variable sampling by using two end-member approaches. First, an equal number of genus occurrences was drawn randomly without replacement from each time interval (occurrence-based rarefaction, as in Miller and Foote 1996 and rarefaction in Alroy et al. 2001). This method assumes that variation in the number of genera in each list is due primarily to differences in the number of specimens sampled locally, not to true variation in local biodiversity (Bush et al. 2004). In the second approach, an equal number of lists (i.e., biofacies) was drawn randomly without replacement from each time interval, irrespective of the total number of occurrences included (list-based rarefaction; UW in Alroy et al. 2001 and Bush et al. 2004). This method assumes that variation in the number of taxa in each list reflects real changes in local richness and that the number of specimens sampled locally remains approximately constant (Bush et al. 2004). The assumptions of neither approach are satisfied here, but they do bracket the optimal subsampling procedure, which involves an exponential weighting of occurrence numbers to reflect accurately the relationship between the number of specimens collected and the number of genera recovered (Alroy 2000; Bush et al. 2004). However, as we will show, the two end-member approaches yield results that are largely congruent.

After subsampling on the basis of occurrences and lists, the apparent stratigraphic range of every subsampled genus was determined from the aggregate subsampled data. This approach is different from that taken by Miller and Foote (1996) and Alroy et al. (2001) because in those analyses, each interval was treated separately and only taxa that were actually subsampled in each interval were counted (sampled within-bin richness), a strategy that is appropriate when there are temporal trends in average genus durations or edge effects related to the ''pull of the Recent'' (Raup 1979). Because these data are less subject to such effects, we calculated sample-standardized total richness, which includes through-ranging genera. However, results are not substantively different if sampled within-bin richness is used instead. Each subsampling routine was repeated 1000 times to estimate expected richness and error. All subsampling analyses were conducted using custom PHP scripts interacting with a MySQL database, but all other calculations were performed using R 2.4.0 for Mac OS 10.4 (R Development Core Team 2006). Throughout, correlations are reported using Spearman rank-order coefficients (r_s). Most correlations will be calculated for time series that have detrended by taking first differences, which pertains only to interval-to-interval variation.

It is worth pointing out that no sampling standardization approach can claim to capture the true underlying macroevolutionary pattern. This is true, if for no other reason, because evenness and rarity also play critical roles in determining the number of taxa that appear in incomplete samples, irrespective of the number of taxa that may actually be present in the target population (e.g., Olszewski 2004). Such attributes of target populations may themselves evolve and are interesting in their own right, but they fall outside the purview of rarefaction and other sampling standardization approaches. The results of this study, and any other study seeking to recalibrate macroevoutionary patterns by standardizing sampling effort, must, therefore, be interpreted strictly as estimates for the parameters that would have been obtained if sampling effort were more or less uniform.

Results

Uncorrected Patterns.—Total crinoid genus richness, estimated on the basis of taxonomically and stratigraphically standardized occurrence data, appears to increase substantially (Fig. 1A), such that genus richness in the most recent O-ES time interval (Telychian, 81 genera) is 37% greater than in the richest Ordovician stage (Rawtheyan, 59 genera). There is no correlation between interval duration and total genus richness ($r_s = -0.08$, $p = 0.75$), indicating that variations in interval duration are not strongly influencing the overall genus richness pattern. Superimposed on this long-term increase in richness is considerable short-term variability, which is highlighted by a prominent spike in richness during the Rawtheyan. Interpreted literally, the uncorrected richness pattern (Fig. 1) suggests that a dramatic diversification of crinoids began in the Middle Ordovician and then continued until at least the Early Silurian, and that the long-term increase in richness was interrupted by several large declines, most notably in the early part of the Late Ordovician and then again in the Hirnantian.

Local, within-biofacies genus richness is highly variable during the O-ES (Fig. 1B), ranging from one to 27, with a mean of four and a median of just two genera per list. Nevertheless, global and local richness are mutually correlated in that they both increase during the O-ES ($r_s = 0.83$). There is, however, no significant correlation between short-term variations in mean local richness and in total global richness within each interval (for first differences, $r_s = -0.36$, $p = 0.14$). This suggests that some component of the long-term increase in global richness that is observed in the uncorrected data may be influenced by an increase in the within-biofacies richness of crinoids, but that shorter-term variations in global richness must be driven by variability in richness at spatial scales above the level of individual biofacies (i.e., between-biofacies and/or regional richness).

Rates of genus extinction and origination in the taxonomically and stratigraphically standardized data are highly variable on an interval-to-interval basis (Fig. 2) and are not mutually correlated (for first differences, $r_s = -0.31$, $p = 0.20$). In the case of extinction, there is no long-term trend, but there is a large increase in the Rawtheyan, which corresponds to the first pulse of the well-known end-Ordovician mass extinction (Eckert 1988; Donovan 1988, 1989; Sheehan 2001). Rates of origination show a significant decrease during the O-ES, but low numbers of genera in the early part of the time series increase the uncertainty of these estimates. Nevertheless, it is clear that a large increase in origination rate, in conjunction with a substantial decrease in extinction rate, is associated with the dramatic late Middle Ordovician increase in genus richness (Fig. 1).

Sampling Standardized Patterns.—Although many important intrinsic biases arising from stratigraphic and taxonomic errors have been ameliorated in these data (Ausich and Peters 2005), the macroevolutionary patterns that they yield are still based on samples and are therefore subject to sampling-related biases. This is particularly true because both the total number of occurrences (Fig. 3A) and the total number of biofacies (i.e., lists) (Fig. 3B) used to calculate these macroevolutionary patterns show a long-term increase and also vary dramatically on a stage-to-stage basis. The num-

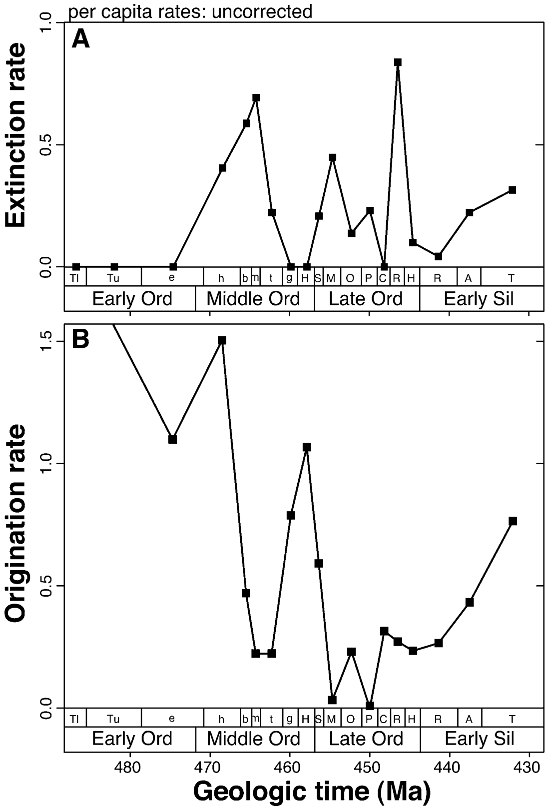

FIGURE 2. Per capita rates of genus extinction (A) and origination (B) in the uncorrected data. Rates are calculated on a per-interval basis using Foote's (2000) survivorship-based rate metrics. Edge effects prohibit calculation of rates in the oldest time interval, but there are no similar edge effects at the end of the time series. Origination rates for the Tremadoc are undefined because of a lack of through-ranging genera.

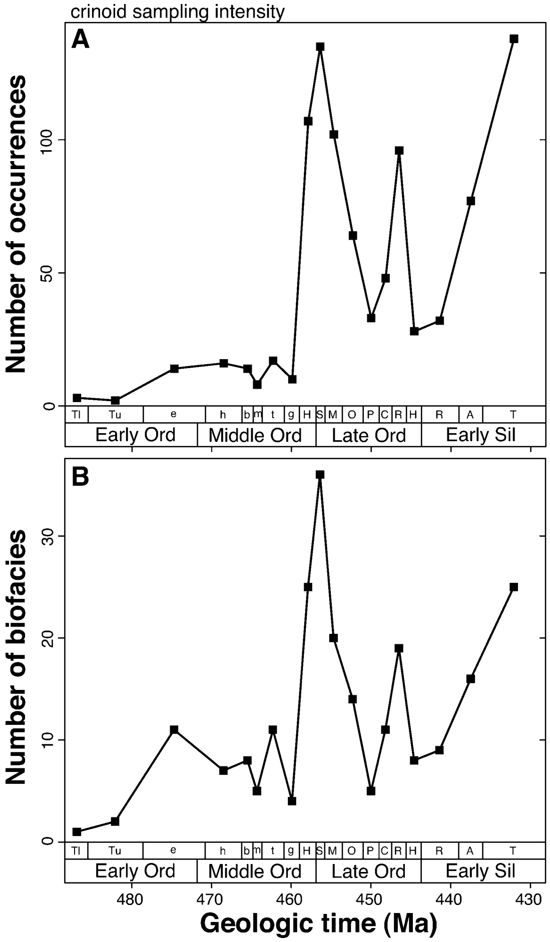

FIGURE 3. Time series of crinoid sampling intensity during the Ordovician and Early Silurian. A, Total number of crinoid occurrences in each time interval. B, Total number of biofacies in each time interval.

ber of formations sampled in each time interval also varies dramatically, but the overall pattern for formations is similar to that for biofacies and is not shown in Figure 3 (there are an average of 1.2 biofacies per formation).

Not surprisingly, there is a strong positive correlation between every measure of sampling intensity and the number of genera recovered in each time interval. This is true both for the raw data and for data that have been detrended by taking first differences (Table 2). Figure 4 shows the nature of the relationship between the number of occurrences and sampled genus richness, which is approximately log-log linear, as expected on the basis of sampling theory (e.g., Alroy 2000). As discussed below, we presume that at least some aspects of the pre–Late Ordovician crinoid occurrence

TABLE 2. Linear product-moment correlation coefficients and *p*-values between sampled genus richness and three measures of sampling intensity. All correlations calculated for natural log-transformed data (Fig. 4).

	Sample size vs. sampled genus richness	
	r	*p*-value
Raw data		
Occurrences vs. genera	0.99	—
Biofacies vs. genera	0.90	—
Formations vs. genera	0.84	—
First differences		
Occurrences vs. genera	0.96	<0.0001
Biofacies vs. genera	0.81	0.0002
Formations vs. genera	0.80	0.0002

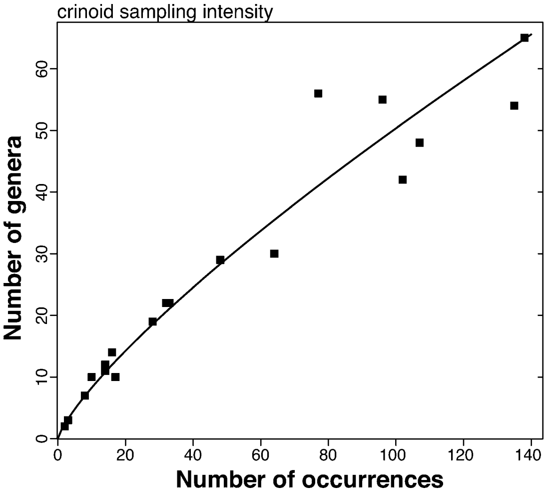

FIGURE 4. Relationship between the number of crinoid genera sampled in a time interval and the number of crinoid occurrences in that interval. The best-fit log-log least-squares linear regression line is shown in arithmetic space. See Table 2 for correlation coefficients for all sampling-richness comparisons.

and richness patterns are representative of a truly depauperate crinoid fauna during this time, and we will focus our standardization efforts on satisfying a minimum quota of occurrences and biofacies in the Late Ordovician and Early Silurian.

Figure 5 shows expected total genus richness, including through-rangers, when an equal number of occurrences (Fig. 5A) or an equal number of biofacies (Fig. 5B) are drawn from each time interval, as described in ''Data and Methods.'' Results are not qualitatively different if sampled within-bin richness (Alroy et al. 2001) is tabulated instead of total richness. The vertical dashed lines in each panel indicate the first time interval for which the minimum subsampling quota was achieved (Fig. 3). Points younger than the dashed line and without error bars in Figure 5B do not meet the subsampling quota.

Although the subsampling results are necessarily based on relatively few occurrences (28) and biofacies (8), there are a number of important differences between the standardized richness pattern and the uncorrected data (Fig. 1). First, the Harnagian diversification, which appears to be quite dramatic in the uncorrected data, is largely maintained after standardizing sampling, even though the

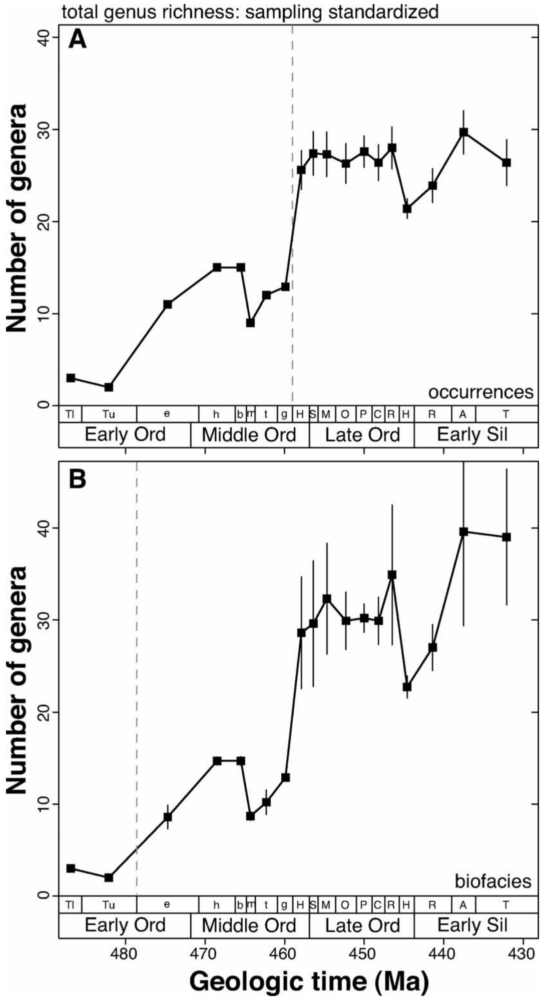

FIGURE 5. Sampling-standardized crinoid genus richness. A, Standardization based on drawing an equal number of occurrences from each time interval (assumes that variation in the number of crinoid genera recovered from each biofacies is due to variation in local sampling effort). B, standardization based on drawing an equal number of biofacies from each time interval (assumes that variation in the number of crinoid genera recovered from each biofacies is due to real variation in local richness). Note that in comparison to the uncorrected richness pattern, these two end-member approaches yield broadly similar results. Mean of 1000 subsampling iterations ± one standard deviation is shown (± one standard error of mean plots within points). Vertical dashed lines show locations in time series where minimum subsampling quota was first achieved.

number of occurrences and biofacies increases dramatically during this time (Fig. 3; there are too few occurrences prior to the Harnagian for meaningful interpretation of the subsampling results). Second, the Harnagian increase is followed by a rise in genus richness no more than

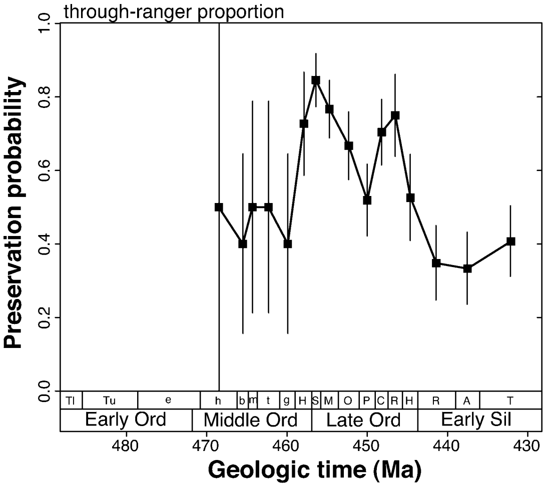

FIGURE 6. Estimated probability of sampling a crinoid genus in each time interval given that a genus is known to span that interval (i.e., through-ranger proportion, which is equal to the proportion of through-ranging crinoid genera that were sampled). The long-term mean rate of recovery is 0.55, but there is considerable short-term variation. Data are not shown for oldest three time intervals because numbers of through-ranging genera are insufficient. Error bars correspond to one standard error of the estimated proportion.

approximately 20%. Finally, and most importantly, there is a significant 25–35% drop in richness during the end-Ordovician extinction, regardless of which subsampling protocol is used, and this decline is followed by a rebound to intermediate richness levels in the Rhuddanian. These two time intervals thus had significantly fewer genera than any other Late Ordovician or Early Silurian time interval (Fig. 5).

The overall long-term genus richness trajectories shown in Figure 5, and in particular in Figure 5A, are difficult to interpret because the sampling quota is necessarily rather small. For example, the plateau in genus richness that appears to be achieved in the Middle Ordovician when occurrences are standardized (Fig. 5A) could reflect the convergence of subsampling curves at small sample sizes rather than constant relative richness. The plausibility of this hypothesis can be evaluated by comparing two time intervals that have comparable levels of sampling but that are widely separated in time. The Soudleyan (Middle Ordovician) and the Telychian (Early Silurian) satisfy these criteria. The latter has about 20% more genera than the Soudleyan, regardless of whether sampled within-bin or total genus richness is considered. The difference in genus richness observed between these two time intervals suggests that occurrence-based subsampling (Fig. 5A) may subdue a long-term increase in genus richness. We therefore favor the standardization based on biofacies (Fig. 5B), which suggests a modest increase in genus richness after the late Middle Ordovician diversification.

The numbers of occurrences, biofacies, or formations that are available in each time interval (Fig. 3) are likely to be good predictors of sampling probability, but when occurrence data are available, gap analysis (Paul 1982) provides a more direct way of estimating those probabilities. Gap analysis makes use of the fact that taxa present before and after a given time interval must have existed throughout the entire duration of that interval. Thus, determining the proportion of through-ranging genera that is recovered provides an estimate of the per-interval probability of sampling, conditioned, of course, on having a total true duration of at least three time intervals and on a genus being preserved at least once in two non-adjacent time intervals.

The average gap-estimated probability of preservation for crinoid genera that satisfy the through-ranging condition is 0.55, which is similar to the frequency ratio estimate of 0.5 per stage provided by Foote and Raup (1996) for Ordovician–Devonian crinoids binned into time intervals approximately twice as long in duration as those used here. Although the average recovery of through-ranging genera is approximately 50% in the O-ES, there is considerable interval-to-interval variation (Fig. 6). Rates of recovery climb as high as 0.85 in the early part of the Late Ordovician and reach a low of 0.33 in the Early Silurian. Overall, short-term changes (i.e., first differences) in through-ranger proportions are significantly positively correlated with the number of occurrences and of biofacies (Fig. 3), but they are not perfectly so ($r_s \sim 0.78$, $p < 0.001$ for both).

Sampling standardization has the desired effect of reducing temporal variation in the through-ranger proportion (results not shown) and, therefore, effective rates of preservation, but even if sampling standardization removed perfectly the effects of variable sampling, true variations in extinction and origination would still be smeared backward and forward in time because of overall recovery probability less than unity. It is therefore necessary to remove the effects of incomplete as well as variable preservation when attempting to recover true extinction and origination histories.

To estimate underlying true rates of extinction, origination, and preservation given only the empirical survivorship matrices derived from the observed genus first and last occurrences, we used Foote's (2003) survivorship-based rate optimization algorithms. Pulsed extinction and origination models were used for the reasons outlined by Foote (2005). In the first set of optimizations, rates of preservation were free parameters fit by Foote's algorithms. Despite the short time series and the relatively few genera that were available to constrain the solutions, rates of preservation fit by Foote's optimization procedure are positively correlated with the empirical through-ranger proportions (for first differences: $r_s = 0.53$, $p = 0.03$). Although the correlation is not strong, the general convergence of two independent approaches to estimating preservation suggests that both are estimating the same parameters. Therefore, we conducted a second rate optimization in which rates of preservation were constrained to be equal to the empirical through-ranger proportions shown in Figure 6 (preservation rates were allowed to vary in intervals for which through-ranger estimates are unavailable). This reduced by almost one-third the number of parameters fit by the model which in turn reduced the error associated with the optimized evolutionary rates.

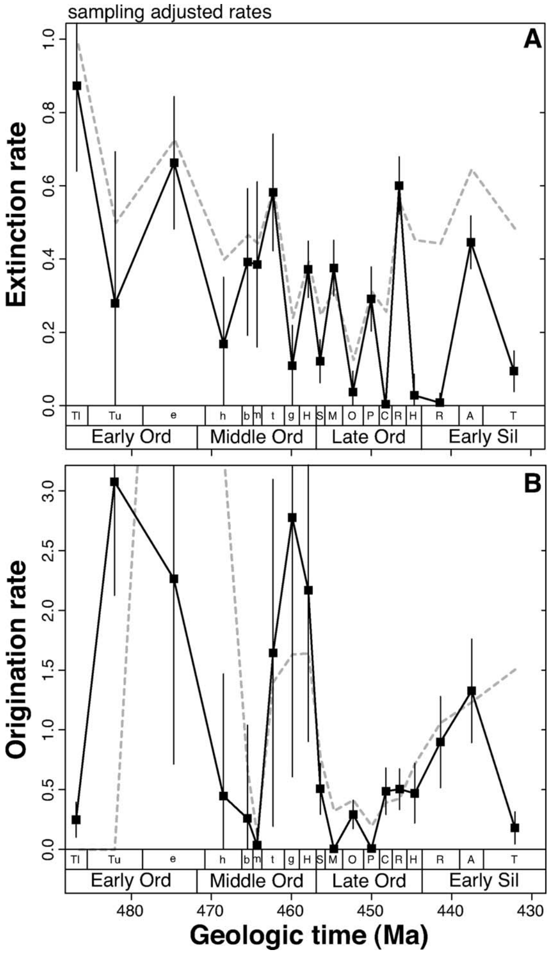

FIGURE 7. Optimized per-interval rates of extinction and origination based on Foote's (2003, 2005) pulsed turnover model. For the solutions shown here, rates of preservation were constrained to equal the through-ranger proportions derived from the occurrence data (Fig. 6). A, Optimized rates of extinction. B, Optimized rates of origination. Gray lines show rate estimates for face-value data (Fig. 2) calculated using the pulsed turnover model. Mean optimized rates and error bars corresponding to ± one standard deviation for 200 iterations are shown.

Preservation-constrained evolutionary rates derived from Foote's optimization procedure are shown in Figure 7. For comparison, the raw time series of extinction and origination from Figure 2, calculated using the pulsed turnover model for comparison, are shown by the gray lines. In principle, differences between the raw rate estimates and the optimized rate estimates are due to variable preservation and to the forward and backward smearing of true variations in rates of turnover (i.e., the Signor-Lipps effect). For example, some of the extinctions that in reality may have occurred during the Rawtheyan would appear to have occurred in the Cautleyan, thereby inflating the extinction rate for this interval. In the case of origination, the optimized solution suggests that some of the originations that actually occurred during the first two Silurian time intervals appear to have occurred during the Telychian, which is consistent with the low rates of through-ranger recovery observed in the first two Silurian intervals (Fig. 6). As did Foote (2003), we found that rates of origination in the uncorrected data have a lower fidelity than do rates of extinction. In the case of extinction, there is a significant positive correlation between first differences in the uncorrected rates and the optimized rates ($r_s = 0.98$; $p < 0.0001$), which reflects the fact that adjusting face-value extinction rates for incomplete preservation modifies the time series, but not so much as to fundamentally change the temporal pattern. Origination rates, on the other hand, are more strongly modified by the rate optimization procedure. The correlation between first differences in uncorrected origination rates and the optimized origination rates is positive, but weaker than that for extinction (excluding Tremadoc, $r_s = 0.59$; $p = 0.02$). We found that Foote's (2003) explanation for the higher fidelity of extinction relative to origination may also apply to crinoids. True peaks of extinction tend to occur during times with high rates of preservation, whereas true peaks of origination tend to occur in intervals with lower preservation rates, thereby subduing peaks of true origination in uncorrected data (cf. Figs. 7, 2). The net effect of such an asymmetry will be a greater distortion of origination relative to extinction.

Foote's (2003) optimized rate estimates for O-ES crinoids demonstrate that much of the apparent short-term variation in rates of extinction and origination is not an artifact of variable preservation. What factors may be driving the macroevolutionary history of crinoids? Foote (2003) and Peters (2005) suggested that many of the original hypotheses for the causes of mass extinctions and other macroevolutionary patterns that were first proposed by Newell (1949, 1952) are correct because many disparate features of the macroevolutionary history of marine animals are reproduced by analogous spatio-temporal patterns in the sedimentary rock record. The possibility that both the environmental dynamics recorded by sedimentary rocks and the macroevolutionary history of marine animals are driven by a common suite of forcing mechanisms has been called the ''Common Cause Hypothesis'' (Peters 2005, 2006a).

To evaluate the Common Cause Hypothesis for O-ES crinoids, we re-tabulated the occurrence-based rate estimates using a binning strategy that permits direct comparisons to area-weighted rates of expansion and contraction of sedimentary rock packages, as calculated by Peters (2005, 2006b). There is good agreement between changes in rates of crinoid extinction and changes in the rates of sedimentary package ''extinction'' (i.e., basin contraction/termination; Fig. 8A). The absolute values of the extinction rates are also similar, but the average crinoid rate is somewhat higher than that for sedimentary packages. There is no similar agreement between rates of crinoid origination and sedimentary package initiation (Fig. 8B).

Discussion

Given only the strong positive correlations between various measures of sampling intensity and the number of genera recovered in each time interval (Table 2, Fig. 4), it would be reasonable to hypothesize that all of the short- and long-term patterns of crinoid genus richness (Fig. 1) might be little more than sampling artifacts and that true genus richness has remained nearly constant throughout the study interval. However, the sampling-standardized richness patterns indicate low richness until the end of the Middle Ordovician, after which time richness remains more or less constant until the end-Ordovician extinction. This pattern of genus richness temporally parallels the expansion of crinoids from hardgrounds to various unconsolidated substrata (Guensburg and Sprinkle 1992; Sprinkle and Guensburg 1995), an ecological transition that may have been facilitated by the evolution of holdfasts suitable for life on soft substrates.

Taphonomic tests for the hypothesis that a true diversification of crinoids occurred during the Middle Ordovician are possible because pelmatozoans are known to occur both on hardgrounds and in unconsolidated sediments throughout the Early and Middle Ordovician. Thus, if crinoids were abundant in soft-substrate communities before the Middle Ordovician, it is likely that they would have

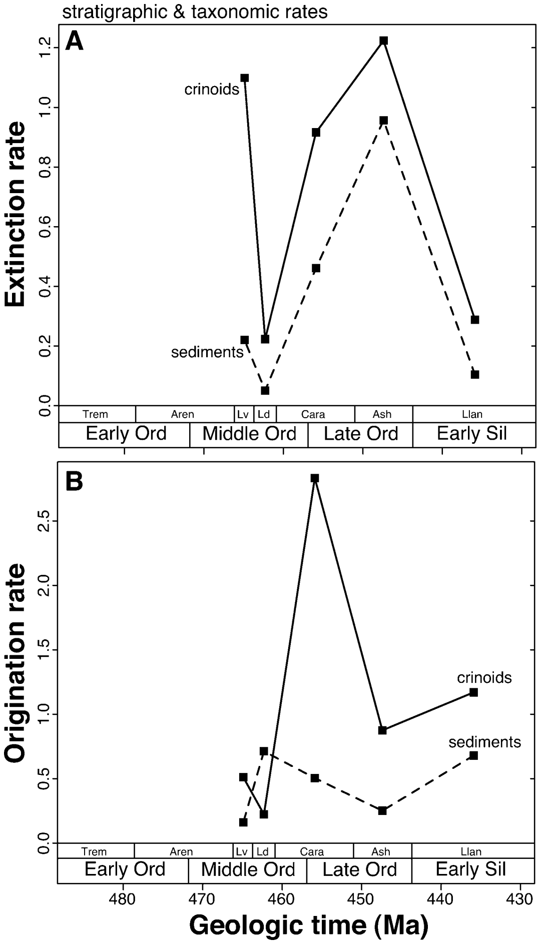

FIGURE 8. Per capita rates of crinoid turnover (solid lines) and per-package rates of sedimentary basin turnover (dashed lines). A, extinction, B, origination. In order to permit direct comparison, both sets of rates have been calculated for Sepkoski's (2002) stages, as opposed to the finer time scale used elsewhere in this study (Table 1). Crinoid rates for the first two stages are undefined and are therefore not shown. There are too few data to calculate reliable correlations, but it is clear that rates of stratigraphic truncation are similar to rates of extinction for crinoids (for first differences, $r_s = 0.80$; $p = 0.33$) and that rates of sedimentary package initiation are not similar to rates of crinoid origination (for first differences, $r_s = 0.20$; $p = 0.92$). See text for discussion.

been frequently encountered in pelmatozoan-bearing biofacies. However, crinoids are not present in many of these assemblages and crinoid abundance and richness remain low until the late Middle Ordovician. Thus, we argue that the sample-standardized pattern (Fig. 5, and in particular Fig. 5B) reflects, at least in a general sense, the actual relative crinoid richness trajectory through this interval.

Newell (1949, 1952), Valentine and Moores (1970), Johnson (1974), Schopf (1974), and Simberloff (1974) were among the first to propose that the expansions and contractions of epi-continental seas may have been dominantly responsible for many of the macroevolutionary patterns observed among marine animals. Most of these discussions focused on species-area effects and the possibility that mass extinctions may have been induced by the elimination of shallow marine environments and their associated ''perched'' endemic faunas. There is now good quantitative evidence to suggest that such factors, as well as correlated environmental changes, have indeed exercised a first-order control on global biodiversity and rates of extinction and origination during the Phanerozoic (Peters 2005, 2006a). This hypothesis is known as the ''Common Cause Hypothesis'' because the pervasive similarities between the rock and fossil records suggest a shared set of forcing mechanisms. The alternative hypothesis, namely that first and last appearances are concentrated at sequence boundaries as a result of sampling failures (Holland 1995, 1996), can be discounted because extinction and origination rates are not equally positively correlated with the rock record (Fig. 8) (Peters 2005), as required by a simple unconformity bias scenario, and because the distribution of gap durations does not predict biological turnover rates (Peters 2006a).

Although the data are presently too few to test rigorously the correlation between sedimentary package turnover and crinoid turnover, the results presented here are congruent with those of Peters (2005), who also found that rates of extinction among marine animals are more strongly correlated with rates of sedimentary package truncation than rates of origination are correlated with rates of sedimentary package initiation. Thus, the results of this study suggest that contractions of epicontinental seas, as well as correlated environmental changes, may have been a primary determinant of extinction among O-ES crinoids. The same is not true for crinoid origination during this time (Fig. 8). Instead, it is probable that biotic factors, such as the acquisition of morphological innovations permitting ecological expansions and interactions with other taxa during the Ordovician radiation (e.g., niche partitioning and tiering) were more important drivers of origination for crinoids. Further work is required to fully test the Common Cause Hypothesis as a dominant forcer of extinction among O-ES crinoids and to establish a range of testable hypotheses for the abrupt radiation that appears to have occurred in the Middle Ordovician, but the new sampling-standardized macroevolutionary history presented here is an important step toward a more nuanced understanding of the drivers of macroevolutionary patterns for an important constituent of many Paleozoic marine communities.

Acknowledgments

We thank M. Foote for graciously applying his rate optimization procedure to these data and for providing helpful feedback. A. M. Bush, C. Brett, and B. Deline provided helpful reviews. Acknowledgment is made to the donors of The American Chemical Society Petroleum Research Fund for partial support of this research to S.E.P. Work partially supported by the National Science Foundation (grants EAR-0544941 to S.E.P. and EAR-0205968 to W.I.A.) and by the National Geographic Society (grant 6789-00 to W.I.A.). This is Paleobiology Database Publication 68.

Literature Cited

Adrain, J. M., and S. R. Westrop. 2000. An empirical assessment of taxic paleobiology. Science 289:110–112.

Allison, P. A., and D. E. G. Briggs. 1993. Paleolatitudinal sampling bias, Phanerozoic species-diversity, and the end-Permian extinction. Geology 21:65–68.

Alroy, J. 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26:707–733.

Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, J. J. Sepkoski Jr., M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversity. Proceedings of the National Academy of Sciences USA 98: 6261–6266.

Ausich, W. I. 2001. Echinoderm taphonomy. Pp. 171–227 *in* M. Jangoux and J. M. Lawrence, eds. Echinoderm studies, Vol. 6. Balkema, Rotterdam.

Ausich, W. I., and S. E. Peters. 2005. A revised macroevolutionary history for Ordovician–Early Silurian crinoids. Paleobiology 31:538–551.

Ausich, W. I., T. W. Kammer, and T. K. Baumiller. 1994. Demise of the Middle Paleozoic crinoid fauna. Paleobiology 20:345–361.

Baumiller, T. K. 1993. Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. Paleobiology 19:304–321.

Bergström, S. M., S. C. Finney, C. Xu, D. Goldman, and S. A. Leslie. 2006. Three new Ordovician global stage names. Lethaia 39:287–288.

Blyth Cain, J. D. 1968. Aspects of the depositional environments and palaeoecology of crinoidal limestones. Scottish Journal of Geology 4:191–208.

Bush, A. M., M. J. Markey, and C. R. Marshall. 2004. Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. Paleobiology 30: 666–686.

Cherns, L., and V. P. Wright. 2000. Missing mollusks as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. Geology 28:791–794.

Crampton, J. S., A. G. Beu, R. A. Cooper, C. M. Jones, B. Marshall, and P. A. Maxwell. 2003. Estimating the rock volume bias in paleobiodiversity studies. Science 301:358–360.

Crampton, J. S., M. Foote, A. G. Beu, R. A. Cooper, I. Matcham, C. M. Jones, P. A. Maxwell, and B. A. Marshall. 2006. Second-order sequence stratigraphic control on the quality of the fossil record at an active margin: New Zealand Eocene to Recent shelf molluscs. Palaios 21:86–105.

Donovan, S. K. 1988. The British Ordovician crinoid fauna. Lethaia 21:424.

———. 1989. The significance of the British Ordovician crinoid fauna. Modern Geology 13:243–255.

Droser, M. L., and S. Finnegan. 2003. The Ordovician radiation: a follow-up to the Cambrian explosion? Integrative and Comparative Biology 43:178–184.

Eckert, J. D. 1988. Late Ordovician extinction of North America and British crinoids. Lethaia 21:147–167.

Eckert, J. D., and C. E. Brett. 2001. Early Silurian (Llandovery) crinoids from the Lower Clinton Group, western New York State. Bulletins of American Paleontology 360:1–88.

Finney, S. 2005. Global series and stages for the Ordovician System: a progress report. Geologica Acta 3:309–316.

Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. *In* D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology*'s perspective. Paleobiology 26(Suppl. to No. 4):74–102.

———. 2003. Origination and extinction through the Phanerozoic: a new approach. Journal of Geology 111:125–148.

———. 2005. Pulsed origination and extinction in the marine realm. Paleobiology 31:6–20.

Foote, M., and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. Paleobiology 22:121–140.

Fortey, R. A., D. A. T. Harper, J. K. Ingham, A. W. Owen, M. A. Parks, A. W. A. Rushton, and N. H. Woodcock. 2000. A revised correlation of Ordovician rocks in the British Isles. Geological Society of London Special Report 24:1–83.

Guensburg, T. E. 1984. Echinoderms of the Middle Ordovician Lebanon Limestone, Central Tennessee. Bulletins of American Paleontology 86.

Guensburg, T. E., and J. Sprinkle. 1992. Rise of echinoderms in the Paleozoic evolutionary fauna: significance of paleoenvironmental controls. Geology 20:407–410.

Holland, S. M. 1995. The stratigraphic distribution of fossils. Paleobiology 21:92–109.

———. 1996. Recognizing artifactually generated coordinated stasis: implications of numerical models and strategies for field tests. Palaeogeography, Palaeoclimatology, Palaeoecology 127:147–156.

———. 2000. The quality of the fossil record: a sequence stratigraphic perspective. *In* D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology*'s perspective. Paleobiology 26(Suppl. to No. 4):148–168.

Holland, S. M., and M. E. Patzkowsky. 1998. Sequence stratigraphy and relative sea-level history of the Middle and Upper Ordovician of the Nashville Dome, Tennessee. Journal of Sedimentary Research 68:684–699.

———. 2002. Stratigraphic variation in the timing of first and last occurrences. Palaios 17:134–146.

Jeffery, C. H. 2001. Heart urchins at the Cretaceous/Tertiary boundary: a tale of two clades. Paleobiology 27:140–158.

Johnson, J. G. 1974. Extinction of perched faunas. Geology 2: 479–482.

Kidwell, S. M., and S. M. Holland. 2002. The quality of the fossil record: implications for evolutionary analyses. Annual Review of Ecology and Systematics 33:561–588.

Kiessling, W. 2005. Habitat effects and sampling bias on Phanerozoic reef distribution. Facies 51:27–35.

———. 2006. Towards an unbiased estimate of fluctuations in reef abundance and volume during the Phanerozoic. Biogeosciences 3:15–27.

Meyer, D. L. 1971. Post-mortem disintegration of Recent crinoids and ophiuroids under natural conditions. Geological Society of America Abstracts with Programs 3:645–646.

Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. Paleobiology 22:304–309.

Newell, N. D. 1949. Periodicity in invertebrate evolution. Geological Society of America Bulletin 60:1911–1912.

———. 1952. Periodicity in invertebrate paleontology. Journal of Paleontology 26:371–385.

Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos 104:377–387.

Paul, C. R. C. 1982. The adequacy of the fossil record. *In* K. A. Joysey and A. E. Friday, eds. Problems of phylogenetic reconstruction. Systematics Association Special Volume 21:75–117. Academic Press, London.

Peters, S. E. 2005. Geologic constraints on the macroevolutionary history of marine animals. Proceedings of the National Academy of Sciences USA 102:12326–12331.

———. 2006a. Genus extinction, origination, and the durations of sedimentary hiatuses. Paleobiology 32:387–407.

———. 2006b. Macrostratigraphy of North America. Journal of Geology 114:391–412.

Peters, S. E., and M. Foote. 2001. Biodiversity in the Phanerozoic: a reinterpretation. Paleobiology 27:583–601.

———. 2002. Determinants of extinction in the fossil record. Nature 416:420–424.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (http://www.R-project.org).

Raup, D. M. 1976. Species diversity in the Phanerozoic: an interpretation. Paleobiology 2:289–297.

———. 1979. Biases in the fossil record of species and genera. Bulletin of the Carnegie Museum of Natural History 13:85–91.

Raup, D. M., and J. J. Sepkoski Jr. 1982. Mass extinctions in the marine fossil record. Science 215:1501–1503.

Schopf, T. J. M. 1974. Permo-Triassic extinctions: relation to seafloor spreading. Journal of Geology 82:129–143.

Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7:36–53.

———. 2002. A compendium of fossil marine animal genera. Bulletins of American Paleontology 363.

Sheehan, P. M. 1977. Species diversity in the Phanerozoic: a reflection of labor by systematists? Paleobiology 3:325–328.

———. 2001. The Late Ordovician mass extinction. Annual Review of Earth and Planetary Sciences 29:331–364.

Signor, P. W., and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geological Society of America Special Paper 190:291–296.

Simberloff, D. S. 1974. Permo-Triassic extinctions: effects of area on biotic equilibrium. Journal of Geology 82:267–274.

Smith, A. B. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. Philosophical Transactions of the Royal Society of London B 356:351–367.

Smith, A. B., and C. H. Jeffery. 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous Period. Nature 392:69–71.

Smith, A. B., A. S. Gale, and N. E. A. Monks. 2001. Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies. Paleobiology 27:241–253.

Sprinkle, J., and T. E. Guensburg. 1995. Origin of echinoderms in the Paleozoic Evolutionary Fauna: the role of substrates. Palaios 10:437–453.

Valentine, J. W., and E. M. Moores. 1970. Plate-tectonic regulation of faunal diversity and sea level: a model. Nature 228: 657–659.

Webster, G. D. 2003. Bibliography and index of Paleozoic crinoids, coronates, and hemistreptocrinoids, 1758–1999. Geological Society of America Special Paper 363.

Wright, P., L. Cherns, and P. Hodges. 2003. Missing mollusks: field testing taphonomic loss in the Mesozoic through early large-scale aragonite dissolution. Geology 31:211–214.